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STYLOBATES LOISETTEAE, A NEW SPECIES OF SHELL-FORMING SEA ANEMONE (COELENTERATA: ACTINIIDAE) FROM WESTERN AUSTRALIA

By

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Abstract: *Stylobates loisetteae* new species, the third species in this genus of deep-water, shell-forming sea anemones, is described. Occurring in seas off the northern coast of Western Australia, at depths of 300–500 m, this new species is symbiotic with a presumably undescribed hermit crab of the genus *Parapagurus*.

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Introduction

Certain species of sea anemones commonly attach to gastropod shells occupied by hermit crabs. As the crustacean grows, it is obliged to exchange its current shell for increasingly larger ones. At least two lineages of sea anemones have the ability to secrete extensions of such shells (carcinoecia) so that the crustaceans presumably need to change abodes less frequently or not at all. The acontiarian lineage includes the European cloak anemone, *Adamsia palliata,* and *Paracalliactis.* The only endomyarian shell-formers known belong in the genus *Stylobates* (family Actiniidae). These anemones can construct large trochoid carcinoecia, an important component of which is chitin (Dunn and Liberman 1983). Each of the two previously described species of this taxon is associated with a different species of *Parapagurus.* Knowledge of this unusual association was summarized by Dunn, Devaney, and Roth (1980).

I describe a third species of *Stylobates* that is symbiotic with an undescribed species of *Parapagurus.* These anemones, like others of the genus, occur only in deep water. The large size attained by their hermit crab associates may be possible at such depths only because their lives do not depend on a supply of sizable gastropod shells. Such shells may be rare in deep water not only because large organisms are less numerous than smaller ones but perhaps more importantly because calcium carbonate dissolves more easily with depth (Correns 1955). Thus, association with carcinoecium-forming actinians may have allowed large hermit crabs to live in an environment they could otherwise not have exploited.

Materials and Methods

I examined 15 alcohol-preserved specimens of actinians and their associated carcinoecia and 5 additional carcinoecia no longer associated with the anemones that made them, all from seas off the northern coast of Western Australia.

Histological sections 8 μm thick were stained with hematoxylin and eosin. Cnidae were measured from seven specimens, although not all tissues of each individual were examined. In the section "Size and distribution of cnidae," n represents the total number of capsules measured, and N is the ratio of the number of animals in which that type of cnida was found to the number examined. Ranges are given for length and width, with measurements for single capsules falling outside the normal range given in parentheses.

Type specimens have been deposited at the Western Australian Museum (WAM), Perth, Western Australia; the Australian Museum (AM), Sydney, New South Wales; and the California Academy of Sciences (CAS), San Francisco, California.

Description

Stylobates loisetteae new species

Base.—Completely adherent to carcinoecium; concave, conforming to its shape. Edge smooth but outline irregular due to curvature of shell. Covers entire shell except for small area at beginning of last whorl (Fig. 1b, 2). Thin, with mesenterial insertions visible as dark lines; color same as that of column.

Column.—Smooth, in preservation colorless to light pink or yellow, ectoderm frequently sloughed off. Diameter to 75 mm. Thin, with mesenterial insertions visible typically as dark lines (Fig. 1a), but insertions of lower orders may be marked in maroon. Occasionally torn, with mesenterial filaments protruding (Fig. 1a). Fosse shallow. Directive axis coincident with shell's axis of coiling. Nearly bilaterally symmetrical, with plane of symmetry perpendicular to directive axis; length on short side 15–30 mm in specimens studied, on long side 25–65 mm. Bulged at shell's apex (Fig. 1a, 2).

Endodermal sphincter (Fig. 3) well-developed, circumscribed, with mesogleal shaft (thick in most) from which arise pinnately arrayed lamellae that may tend to a reticulate pattern (Fig. 3a); ovoid (Fig. 3a) to deltoid (Fig. 3b) in cross-section. Presumably weak, to judge by expanded oral disc and exposed tentacles in all specimens examined.

Oral Disc and Tentacles.—Oral disc flat, to 55 mm diameter; color same as that of column. Round, central mouth typically agape in preserved specimens (Fig. 1a). Marginal tentacles thin, pointed (Fig. 1, 2); inner ones to 20 mm long, progressively shorter marginally; about 160 total counted in one medium-sized specimen, nearly 200 in a large one.

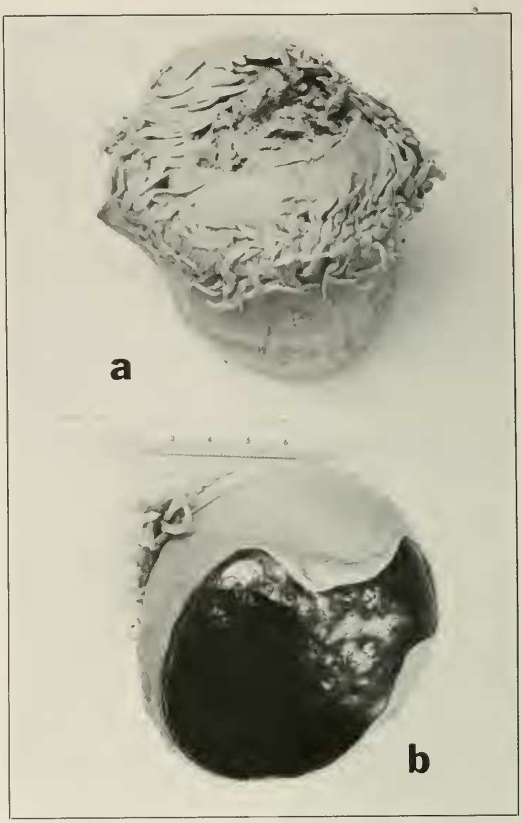

Figure 1. Paratype specimen of *Stylobates loisetteae* (WAM 21-84). Note that pedal disc envelops entire carcinoecium save for that portion at beginning of ultimate whorl.

Ectodermal musculature longitudinal in tentacles, radial in oral disc.

Mesenteries and Internal Anatomy.—Mesenteries thin; no stomata seen. At least first two orders complete; five or six cycles in individuals of average size. Retractor muscles moderately well developed, diffuse (Fig. 4); occasional muscle bundles sunken into mesoglea. Parietobasilar muscles poorly developed. Mesenteries of two highest orders gametogenic; sexes presumably separate—only females seen. All developmental stages of ova may occur in a single mesentery; ova in section to 950 μm diameter.

Actinopharynx shallowly ribbed, with two symmetrical siphonoglyphs.

FIGURE 2. Paratype specimen of *Stylobates loisetteae* (AM G 15227).

CARCINOECIUM.—Varies from thin chitinous coating on large gastropod shell (Fig. 5), to massive trochoid carcinoecium (Fig. 1, 2) produced entirely by actinian except for minute apical snail shell. Maximum diameter of actinian-produced carcinoecium among material examined 85 mm with aperture 40 × 55 mm (WAM 18-84). Golden color and gloss, although alcohol-preserved specimens tend to dull and turn chalky when dried. Umbilicus shallow to absent.

CNIDOM.—Spirocysts, basitrichous isorhizas (basitrichs), microbasic *p*-mastigophores.

Size and distribution of cnidae (letters refer to components of Fig. 6).

Tentacles

spirocysts (a) 21.1–55.8 × 2.5–3.7 μm
n = 63 N = 6/6

basitrichs (b) 29.8–39.7 × 2.5–3.7 μm
n = 70 N = 6/6

FIGURE 3. Cross-section of sphincter muscles of *Stylobates loisetteae* (a: paratype WAM 21-84; b: holotype WAM 18-84). Scale = 500 μm.

FIGURE 4. Cross-section through mesenteries of *Stylobates loisetteae* (holotype WAM 18-24). Note retractor muscles and ova. Scale = 1 mm.

basitrichs (c) 9.9–16.1 × 1.6–2.5(4.0) μm
n = 11 N = 3/6

Actinopharynx
basitrichs (d) 26.0–37.2 × 2.5–3.7 μm
n = 59 N = 5/5

Column
basitrichs (e) 21.1–33.5 × 2.5–3.7 μm
n = 46 N = 5/5

Mesenterial filaments
basitrichs (f) 28.5–37.2 × 4.7–6.0 μm
n = 34 N = 5/7
basitrichs (g) 28.5–37.2 × 2.5–3.5 μm
n = 11 N = 3/7
basitrichs (h) 12.4–16.1 × 1.9–3.1 μm
n = 10 N = 4/7
microbasic *p*-mastigophores (i)
23.6–32.2 × 3.5–6.2 μm n = 50 N = 7/7

With one exception in the seven specimens examined, an individual possesses either wide (f) or narrow (g) basitrichs in its mesenterial filaments.

Type Specimens and Locality

HOLOTYPE.—One female specimen on empty shell, WAM 18-84 (Fig. 3, 4), collected by Loisette M. Marsh at 18°41′S, 116° 45–47′E (station SO2/82/46, 145 nautical miles (269 km) NW of Port Hedland, Western Australia), at 506–508 m from a muddy bottom, on 13 April 1982; along with histological sections—five slides of the sphincter and five of mesenteries.

PARATYPES.—Two specimens, each on an empty shell, WAM 21-84 (Fig. 1, 3), collected by P. Berry and N. Sinclair at 18° 06′S, 118°10′E (station COR/83/04, SW of Imperieuse Reef, Rowley Shoals, Western Australia), at 353–356 m from a muddy bottom, on 17 August 1983; along with histological sections from one specimen—five slides of the sphincter and five of mesenteries.

One actinian and its carcinoecium (separated), WAM 177-83, collected by Loisette M. Marsh at 18°20′S, 118°00′E–18° 19′S, 118°01′E (station SO2/82/37, 124 nautical miles (230 km) NNW of Port Hedland, Western Australia), at 320 m, on 10 April 1982; along with histological sections—four slides of the sphincter and three of mesenteries.

Six actinians (four on shells containing hermit crabs, one on an empty shell, and one detached) plus a naked, empty shell, CAS 052762, collected by P. Berry and N. Sinclair at 18°06′S, 118°10′E (station COR/83/04, SW of Imperieuse Reef, Rowley Shoals, Western Australia), at 353–356 m from a muddy bottom, on 17 August 1983; along with histological sections from one specimen—six slides of the sphincter and five of mesenteries.

Five specimens, each on a shell, two of which are occupied, AM G 15227 (Fig. 2), collected by P. Berry and N. Sinclair at 18° 05′S, 118°10′E (station COR/83/02, SW of Imperieuse Reef, Rowley Shoals, Western Australia), at 400–401 m from a muddy bottom, on 17 August 1983; along with histological sections from one specimen—five slides of the sphincter and five of mesenteries.

Three dry shells (one with a thin chitinous coating, one with a thick chitinous coating and a half whorl extension, and a high-spired coated one with nearly a full whorl of trochoid chitinous extension) CAS 052763 (Fig. 5), collected by Loisette M. Marsh, NW of Port Hedland, Western Australia (precise locality unknown) in April 1982.

ETYMOLOGY.—*Stylobates loisetteae* honors Loisette M. Marsh, Curator in the Department of Marine Zoology of the Western Australian Museum, for her many contributions to the natural history of the eastern Indian Ocean, and for her admirable concern in sending specimens from the Western Australian Museum to interested scientists.

GEOGRAPHICAL DISTRIBUTION.—Twenty-nine specimens of this species have been collected under the auspices of the Western Australian Museum near Port Hedland and Imperieuse Reef—in the area 18–19° S and 117–118.5° E—at depths of 300–500 m. Bottoms where these animals were dredged are characterized as muddy.

Discussion

Differential Diagnosis

Comparisons with the other species of *Stylobates*—*S. aeneus* and *S. cancrisocia*—are based on data in Dunn, Devaney, and Roth (1980). Carcinoecia of *S. loisetteae* vary more than those of *S. aeneus*. This may be related to the nature of the original gastropod shell, which in *S. aeneus* is always very small, so that the carcinoecium is almost entirely a production of the anemone. By contrast, a high proportion of the *S. loisetteae* specimens examined (and the only one of *S. cancrisocia*) occur on large shells, which the anemone coats with chitinous material. Extensions of these shells, although invariably trochoid regardless of the shell's morphology, are frequently of uneven diameter and thickness. Carcinoecia entirely produced by actinians of the new species, despite being thicker and firmer than those of the other two species, may be knobby and bumpy. Growth lines of *S. loisetteae* carcinoecia, whether entirely produced by the actinian or on a large gastropod shell, may be wavy, in contrast to their concentricity in *S. aeneus*. The carcinoecium of *S. aeneus* has a deep umbilicus, unlike that of *S. loisetteae.*

Orientation of the actinian on the carcinoecium differs as well. Looking down upon the three-part symbiotic unit as it would be in life with the hermit crab extended from the carcinoecium, the apex of the shell is on the crustacean's right side and the actinian's tentacle crown faces rearward (the orientation of the specimen in Figure 2 is precisely upside down of this). In *S. aeneus,* the tentacle crown is on the parapagurid's left side (fig. 1b in Dunn, Devaney, and Roth 1980). It appears from Carlgren's (1928, plate II, fig. 6–9) illustrations that the oral disc of *S. cancrisocia* occupies a position even nearer the carcinoecium's aperture than it does in *S. aeneus,* being almost directly beneath the mouth of the parapagurid. This orientation so resembles that of the hormathiid anemone *Adamsia palliata* with respect to its host, *Pagurus prideauxi,* that Carlgren (1928) named the genus *Isadamsia* (see Dunn, Devaney, and Roth 1980, for discussion of nomenclature).

Nematocysts also differentiate *Stylobates loisetteae* from the two previously described species, with allowance made for the data on *S. cancrisocia* cited by Dunn, Devaney, and Roth (1980) having been taken from a single individual. Spirocysts (Fig. 6a) are broader in both other species, particularly *S. aeneus.* Large tentacle basitrichs (Fig. 6b) are smaller in *S. cancrisocia.* Small tentacle basitrichs (Fig. 6c) were not found in either of the other species. Only *S. aeneus* is reported to possess small basitrichs in the actinopharynx.

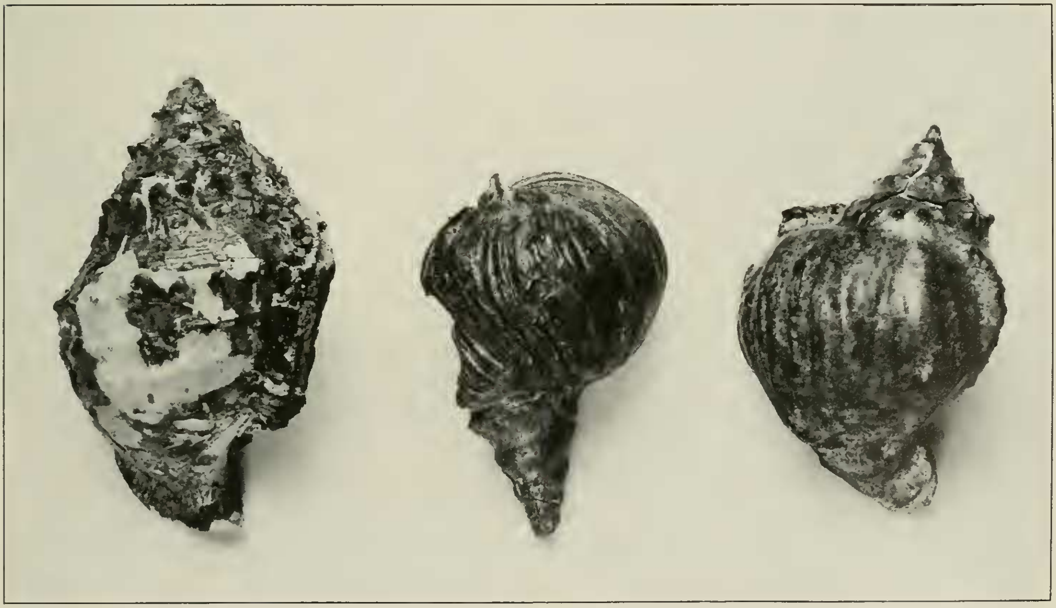

FIGURE 5. Three dry carcinoecia of *Stylobates loisetteae* (paratypes CAS 052763). That at left is a massive shell covered by a thin veneer of chitinous material. The coating on the right-hand specimen is thick and extends for half a whorl beyond the lip of the gastropod shell. The actinian extended the carcinoecium on the high-spired shell at center for nearly a full whorl; note that the actinian-produced portion is trochoid, regardless of the geometry of the founder gastropod shell.

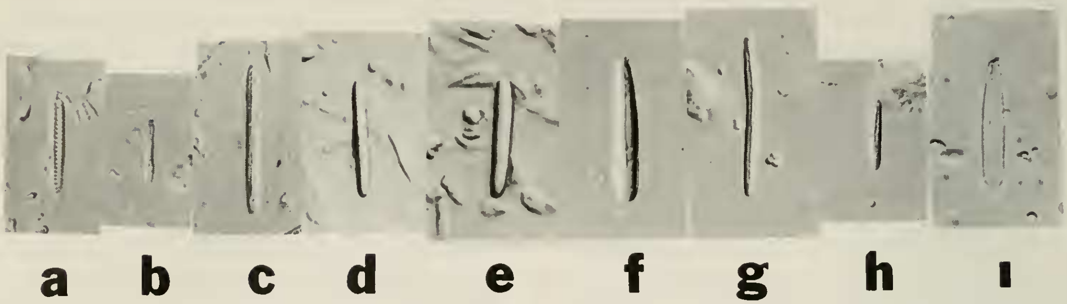

FIGURE 6. Cnidae of *Stylobates loisetteae*. Scale = 10 μm. Refer to text for explanation.

Column basitrichs (Fig. 6e) tend to be larger in *S. aeneus,* there being more overlap with *S. loisetteae* than with *S. cancrisocia.* The larger filament basitrichs are of similar length in all three species, but those of *S. cancrisocia* are broad (like Fig. 6f), whereas those of *S. aeneus* appear to be entirely of the narrow form (like Fig. 6g). The smaller filament basitrichs (Fig. 6h) tend to be larger in *S. aeneus.* Microbasic *p*-mastigophores of the filaments (Fig. 6i) are smaller in *S. cancrisocia.*

Natural History

The symbiont of *Stylobates loisetteae* is an as yet undescribed species of *Parapagurus* (Marsh pers. comm.). *Stylobates aeneus* is associated with *P. dofleini,* and *S. cancrisocia* with *P. trispinosus.* Thus there appears to be species specificity in this exclusively deep-water relationship. Moreover, the three known species of *Stylobates* are distributed allopatrically.

I have found the body wall of living specimens of *Stylobates aeneus* to be unusually thin and easily ruptured, in contrast to the typically thick, tough columns of deep-water actinians. The walking legs of *Parapagurus dofleini* are notably long; indeed, the word *stylobates* means "a walker on stilts" (Dunn, Devaney, and Roth 1980). Long legs allow the hermit to carry its carcinoecium (and associated anemone) well above the substratum, thereby making the delicate actinian, which is vital to its partner's continued existence, less vulnerable to injury. The situation in *S. cancrisocia* is unclear, and I have been unable to reexamine the one known specimen (see Dunn, Devaney, and Roth 1980), but the position of the anemone's oral disc, beneath the hermit's mouth, suggests that the hermit must hold the actinian aloft.

The initial portion of the ultimate whorl of the carcinoecium is exposed in every specimen of *Stylobates loisetteae* examined, and several bear evidence of that surface having been abraded or scuffed. This is perhaps unremarkable since it is the ventralmost portion of the shell, but it differs from *S. aeneus* (many tens of which I have examined, alive and preserved). I infer from this that the parapagurid carries its carcinoecium very low, or even drags it along the substratum, as hermit crabs commonly do. If the anemone were oriented on the carcinoecium as is *S. aeneus,* the oral disc would be scuffed against the substratum and the tentacles possibly snagged. I posit the rearward displacement of *S. loisetteae* to be an associated adaptation to raise the tentacle crown and thereby protect the thin-walled anemone.

Carlgren's (1949:60) definition of *Isadamsia* includes the sentence "The species of the genus live in symbiosis with hermit crabs in such a way that their mouths are always situated beneath that of the hermits (as in *Adamsia*)." However, he remarks (p. 95) that the various species of *Paracalliactis* differ in the positioning of their mouth relative to that of their hermit. Clearly the precise orientation of the anemone on the carcinoecium is not a feature of generic significance but is a specific coadaptation to a partner's habitus.

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